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BOOK REVIEW

TURNER'S CONCISE ENCYCLOPEDIA OF TROPICAL TREE BIOLOGY[1]

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> Poets and moralists, judging from our English trees and fruits, have thought that there existed an inverse proportion between the size of the one and the other, so that their fall should be harmless to man. Two of the most formidable fruits known, however, the Brazil Nut (*Bertholletia*) and the Durian, grow on lofty trees, from which they both fall as soon as they are ripe, and often wound or kill those who seek to obtain them. From this we may learn two things:—first, not to draw conclusions from a very partial view of Nature; and secondly, that trees and fruits and all the varied productions of the animal and vegetable kingdoms, have not been created solely for the use and convenience of man.
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> —A. R. Wallace, 1856

There are some 50–60 000 described species of arborescent woody plants found in the world's tropical rain forests. Comprising nearly a quarter of known higher plants, these leafy organisms are the main structural elements of the world's most diverse—and most threatened—ecological systems. The biology of tropical trees is thus of central interest and importance to both conservationists and to those charged with managing tropical forests for timber and other renewable resources. Beyond such applied perspectives, tropical trees are tremendously fascinating organisms in and of themselves. The immense diversity of tropical trees continues to amaze biologists and has inspired a wealth of basic ecological research on the mechanisms that generate and maintain diversity in ecological systems generally. In addition, tropical trees present continuing challenges and surprises to students of phytochemistry, physiological ecology, plant–animal interactions, evolutionary biology, and ecosystems science.

A number of recent texts and edited volumes address the broad topic of tropical forest ecology. T. C. Whitmore's *An introduction to tropical rain forests, 2nd edition* (1998) is a well-constructed and accessible introductory text. M. Kellman and R. Tackaberry's *Tropical environments: the functioning and management of tropical ecosystems* (1997) is a broader and more agriculturally oriented introduction to the topic. P. W. Richards' weighty second edition of *The tropical rain forest* (1996) remains the standard reference work in the field and is particularly valuable as a key to the older literature. Recent volumes have also explored in detail the ecology and natural history of a handful of well-studied tropical forests (e.g., McDade et al., 1994; Leigh, Rand, and Windsor, 1996; Struhsaker, 1997; Leigh, 1999). However, with the exception of an edited collection published almost 25 y ago (Tomlinson and Zimmermann, *Tropical trees as living systems* [1978]), there has been a notable absence of any treatise that specifically covers the ecology and organismic biology of tropical trees.

Ian Turner, working out of the venerable Singapore Botanical Gardens—the previous professional home of such botanical notables as E. J. H. Corner, R. E. Holttum, and H. N. Ridley—has produced such a book "*. . . written with the aim of summarising contemporary understanding of the ecology of tropical rain-forest trees, with particular reference to comparative ecology*" (p. xi). This is an important task and timely. Through the 1980s most detailed studies of tropical tree ecology were limited to a very few species, with most work conducted at a few sites in Central America. The 1990s witnessed a veritable explosion of research on tropical trees, with a much wider geographic focus. In particular, many studies have now been undertaken in or near the geographic centers of tropical tree diversity in Amazonia and the Sundaland region of Southeast Asia. Both the proliferation of studies and geographic shift are well illustrated by the references cited in Turner's book (Fig. 1). Fully two-thirds (564/854) of Turner's references are to studies published in the 1990s. Studies conducted in South America and Sundaland make up nearly half of the recent site-specific references, compared to approximately 25% of the 1980s literature. Incidentally, the exponential rise and geographic diversification in studies of tropical trees is likely to continue through the next decade, with more than 10% of the world's described tropical tree species now being monitored in large, permanent forest plots distributed throughout the Neotropics, Africa, and Asia (Burslem, Garwood, and Thomas, 2001).

Fully summarizing all aspects of the ecology of a quarter of the planet's higher plants would be a truly immense task. However, the scope of Turner's book is in fact somewhat narrower than it might first appear. The work focuses on the organismic biology of tropical trees, essentially covering tree establishment, growth, demography, functional morphology, reproduction, and interactions with other trophic levels. Discussions of most topics are also generally well grounded in terms of physiological processes and mechanisms. Some aspects of population ecology are addressed (e.g., life tables); however, community-level aspects of tropical tree ecology are touched upon only tangentially. You will find no dominance-diversity curves here, and even species-area curves are described only once in the introduction. Landscape ecology, an area of intense recent research activity in the tropics (and to which Turner himself has made valuable contributions) is also ignored. Ecosystem-level ecology is likewise not part of the picture, at least directly. Enthusiasts of forest fragmentation biology, carbon flux, or nitrogen dynamics will thus have to seek satisfaction elsewhere.

Although not spanning the vast whole that is ecology, Turn-

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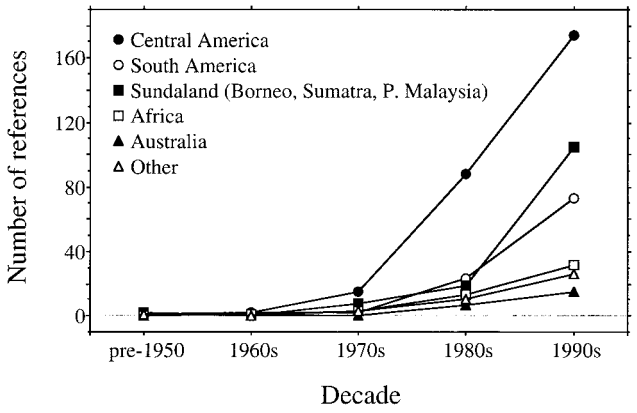

Fig. 1. Geographic location of site-specific studies cited by Turner, illustrating the exponential increase in studies of tropical tree ecology generally and the shift in geographic emphasis from Central America to centers of tropical tree diversity in South America and the Sundaland region of Southeast Asia.

er's synoptic treatment of the organismic and comparative biology of tropical trees is both competent and impressively comprehensive. However, the book can approach such completeness while remaining modest in bulk only by making some major compromises. First and foremost, the book assumes a great deal of background expertise of its readers. Second, it presents the results of most studies in a telegraphic style that often emphasizes only one or two major points of a given paper. In the latter respect, Turner's book sometimes reads very much like one of those traditional Germanic literature reviews, in which each paper summarized is allocated one or two sentences only. This is not meant as a dire criticism: such reviews can be exceedingly useful, and their preparation is now something of a lost art, at least in the English language literature. Moreover, Turner's book is not simply a string of unrelated paper synopses: it is well organized by topic, and provides effective syntheses of many important questions. A better description of the book might thus be a series of well-written introductions to primary research papers addressing different aspects of the organismic biology of tropical trees.

So, what specifically have we learned about tropical trees in the last decade? First of all, we've dispelled some tropical tree myths. We've learned that tropical trees are not always shallow-rooted; roots have been recorded at soils depths of up to 18 m in Amazonian forests (Nepstad et al., 1994). Seed germination mediated by shifts in light quality was considered a litmus test for a ''pioneer'' regeneration strategy by some; however, it seems that light-mediated germination may be quite rare among all ecological groups of tropical trees (Kyereh, Swaine, and Thompson, 1999). Trees characteristic of nutrient-deficient heath forests were thought to have tough leaves as an anti-herbivore adaptation; recent biomechanical studies have shown that canopy leaves in mesophytic forests are actually as tough as those of heath forest species (Turner et al., 1993). Perhaps of broader interest are changes in generalizations on the predominance of tight coevolutionary relationships in tropical forests. Although figs and fig-wasps do represent such a tight mutualistic relationship, figs are an exception, and one-to-one pairings between tropical trees and either their pollinators or seed-dispersers are very rare. Even the famous dodo example has been challenged. The Mauritian endemic tree *Sideroxylon grandiflorum* was thought to be approaching extinction due to the absence of its major disperser, the dodo (*Raphus cucullatus*); but it has recently been found that unabraded seeds, and those consumed by giant tortoises, may successfully germinate and establish (Witmer and Cheke, 1991).

The scope of the book is such that even die-hard tropical tree aficionados are certain to learn something new. For example, I was intrigued to learn of recent evidence for secondary seed dispersal by ants in the Neotropics (e.g., Pizo and Oliveira, 1998), of the recent discovery of a cockroach pollination syndrome (Nagamitsu and Inoue, 1997), and of obligate bacteria–plant symbioses in understory treelets within many species of Rubiaceae and Myrsinaceae (Miller, 1990). Some intriguing comparisons are also made to trees in biomes outside the tropics. One such item that especially grabbed my interest was work on latitudinal gradients in leaf morphology and venation patterns—including the interesting speculation that the tendency toward toothed leaf margins in temperate trees is a consequence of a relaxed constraint on hydrological supply near the outer leaf margin in deciduous species (Roth et al., 1995).

The book is lucidly written and well produced overall. Figures, tables, and illustrations are well chosen and include a few black and white prints of remarkable canopy pollinator photographs by the late Tamiji Inoue (who has, in Asia, a status similar to the departed tropical naturalist Al Gentry). Some of the figures are a bit clumsily copied from primary research articles, but I detected only one serious goof (mixed-up legends in fig. 4.7). As is absolutely necessary for a book of this type to be truly useful, the indices are exemplary. Kudos are clearly due to Cambridge University Press on this count (other academic publishers PLEASE take note!).

If it is not apparent from the foregoing, let me be blunt: this is no coffee-table book. The high level of biological vocabulary and background assumed by the author may effectively limit the audience to other researchers and the most serious of students. Technical terms are often used without definition or citation to background-related or introductory material. Moreover, little or no attempt is made to describe or characterize the panoply of obscure tropical trees and other organisms referred to by scientific name only. To give some flavor of the level of background assumed, terms ranging from agamospermy, amenochore, autocorrelation, and boundary layer, to microfibrallar angle, phanerocotylar, tension wood, and work of fracture, are all used without apology. Fortunately, readers are provided with in-text definitions for some bona-fide ten-dollar terms and concepts, such as brochidodromous, hapaxanthy, sapromyiophily, and trichromacy. As far as natural history background is concerned, one's understanding and appreciation of the book will be greatly enhanced if you have a passing familiarity with at least some well-known tropical tree taxa, such as *Cecropia*, *Ficus*, *Macaranga*, *Piper*, and *Shorea*. Of course, it's very much better if, as you read the sentence ''Compound leaves are common, including some quite bizarre forms such as those found in members of the Araliaceae'' (p. 60), the peculiar understory treelet *Trevesia burckii* comes immediately to mind! If the only plant genus you know by name is *Arabidopsis*, then you'd better read Turner with Mabberly's *The plant book* (1997) close at hand.

The main goal of Turner's text, as stated at the outset by the author, is ''summarising current understanding.'' No particular effort is made to establish a clear theoretical framework

or to construct a hierarchy of research questions. Rather, by reviewing recent work in a comprehensive manner, the author seems to have hoped that a new synthesis might simply emerge of its own accord. In retrospect, at least, Turner himself seems to have realized that this was a somewhat naïve hope, given the complexity of tropical forests (and perhaps also the nature of scientific syntheses generally). The book ends rather abruptly with the following paragraph:

> One of my objectives when I set out to write this book was to see if there was a new synthesis of the comparative ecology of tropical trees awaiting discovery amidst the voluminous literature on tropical rain forests. I have failed to find a new synthesis. This is very likely to be a reflection of my own shortcomings, but I also believe that it is testament to the complexity of the ecology and evolution of the tropical rain-forest community. Scientists like simple, elegant solutions to problems, but rain forests just do not work that way. *(p. 247)*

One may take this statement at face value. However, another way to look at Turner's conclusion is as a challenge: perhaps some kind of novel synthesis is actually buried amongst the details. In this regard, one generalization that certainly seems to emerge from this book—that is in fact reflected in one way or another on each and every page—is that tropical tree species, even closely related ones, tend to differ from one another in a multitude of ways. Tropical trees vary greatly in terms of their architecture, mycorrhizal status, leaf morphology, antiherbivore defenses, rates of photosynthesis, growth, and mortality, mating systems, flowering patterns, pollination and seed dispersal syndromes, seed size, patterns of seed and seedling development, shade tolerance, and leaf lifespan. Much of Turner's book may be viewed as a detailed chronicle of these differences. It is an interesting testament to the decline of niche-based ''equilibrium'' theories of species coexistence in ecology that such a pervasive pattern of ecological differences among tropical trees could go almost completely unremarked in a book on tropical tree ''ecology.''

Although it lacks anything more than a superficial overview of the potential role of tree ''niches'' in structuring tropical forest communities, Turner's book concludes with an exploration of the broad patterns of covariation among ecological traits in tropical trees. Here is where the synthetic interest really lies. With regard to the ''pioneer-climax'' gradient in tree regeneration strategies, Turner effectively highlights proposed differences that are well supported (e.g., pioneer trees tend to have small seeds, rapid photosynthesis and growth, and pale wood of low density), from those that aren't (e.g., pioneers do not rely mostly on nitrate as a source of N; their germination is not generally light triggered). He also emphasizes the importance of other kinds of ecological differentiation that have received less attention in the literature. Chief among these is tree size (i.e., the ''shrub-emergent'' gradient in tree life histories), which has received considerable recent attention as a correlate of growth, reproduction, and allometry (e.g., Davies and Ashton, 1999; Thomas and Bazzaz, 1999). It remains unclear, however, to what degree the ''pioneer-climax'' gradient and the ''shrub-emergent'' gradient are orthogonal. For example, the occurrence of ''giant invader'' species, including such economically important species as mahogany (*Swietenia macrophylla*) (although perhaps better exemplified by *Ceiba pentandra* or *Alstonia* spp.), makes it abundantly clear that not all ''pioneers'' are small in stature. Also, while Turner emphasizes size and shade tolerance, there may be other equally important but overlooked axes of ecological variation in tropical trees. In particular, the ecological and physiological correlates of edaphic preferences remain an outstanding problem that Turner doesn't really address.

As a ''celebration of diversity,'' Turner's book is in important respects the antithesis of another prominent book published this year. Stephen Hubbell's *The unified neutral theory of biodiversity and biogeography* (2001) is a search for ecological generalizations that proceeds by making the extreme but theoretically useful assumption that tropical trees are exact ecological duplicates. This willful treatment of tropical trees as ecological caricatures results in some surprisingly accurate predictions regarding ecological patterns at higher levels of integration, such as species-area curves and dominance-diversity relationships. Interestingly, these community-level patterns are precisely those omitted from Turner's account. Late in *The unified neutral theory* Hubbell does try to reconcile his null model with the overwhelming evidence that tropical trees (and other organisms) do in fact show large ecological differences. The case is made that tropical trees are essentially arrayed on a single ecological axis related to shade tolerance, which results in identical per-capita recruitment rates among species. Is this necessarily so? And what of other kinds of ecological differences, such as those related to size or edaphic preference? I suspect that the obvious contradictions between the ''Turnerian'' and ''Hubbellian'' views will be a main theme in tropical tree research for the next decade or so, at the least.

Turner's book will clearly be of interest to tropical forest ecologists, but does *The ecology of trees in the tropical rain forest* deserve an audience broader than those already obsessed with arborescent organisms of the torrid zone? I would emphatically argue yes. Though Turner doesn't emphasize this point, studies of tropical tree biology have in some respects outpaced work in the temperate zone. For example, we have generally more detailed information available on tropical tree pollination systems than those of temperate trees (as a case in point, we don't know what pollinates Canada's national emblem, *Acer saccharum*)! Similar examples are found in areas as diverse as the chemistry of natural defenses, quantitative analyses of life history variation, analyses of size-dependent growth and reproduction, and the physiological basis for shade tolerance. Thus, researchers and students mainly interested in temperate forest ecology will certainly find much of interest and relevance in a close reading of Turner's book. More broadly, one should keep in mind the historical importance of tropical diversity in biology, as the source of patterns that gave us the theory of natural selection via Darwin and Wallace, and plant biogeography via Humboldt. As Wallace noted almost 150 yr ago, knowledge of tropical trees is critical in correcting a ''very partial view of Nature'' that can result in serious misapprehensions regarding patterns and processes in biology. It would not at all be surprising if 21st century syntheses in ecology and evolutionary biology emerge from the diversity and complexity of tropical forests.

There is one ultimate test very specific to books on tropical ecology. This test lies in the answer to the following question: if a tropical ecologist is departing for an extended period to a remote field site, will she pack this book? Only a very few carefully selected items will make it in the bulging rucksack, since anti-malarials, leech socks, and plant presses must in-

evitably take precedence, and field guides and identification manuals will almost certainly be next in line. Although Turner's encyclopedia may not qualify as light reading (to be consumed between bouts of tropical fever), it has the distinct advantage of being compact. Ounce per ounce, it will probably have the highest information contact of any item in the luggage (at least those not in binary form). My prediction is that the book will in fact make it in—perhaps wedged in the mosquito netting next to its nemesis in the form of Hubbell's book—thus receiving the highest possible accolade that can be given such a work.

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